

NESTING, MATING AND FORAGING HABITS OF *MELISSODES*
(*MELISSODES*) *TEPIDA TEPIDA* CRESSON IN IDAHO
(HYMENOPTERA: ANTHOPHORIDAE)

D. C. TRIPLETT AND A. R. GITTINS

Division of Entomology, University of Idaho, Moscow, Idaho 83843.

Abstract.—Field studies are reported on nest construction, mating, and female foraging behavior of *Melissodes tepida tepida* Cresson, at two nesting sites in southwestern Idaho. Females form loose nesting aggregations but construct and provision individual burrows in the ground. Adult males exhibit protandry and their flight activity approaches territorial behavior patterns. *Melissodes tepida tepida* is a polylectic subspecies visiting a number of different host plants for pollen as well as nectar.

Key Words: flower bee, native bee biology, protandry, groundnesting.

Studies of wild bee species, especially those which evidence potential for population enhancement and management, form an integral part of a continuing research program for pollination of seed crops in Idaho. *Melissodes tepida tepida* Cresson, an aggregate nester, frequently found in seed growing areas of southwestern Idaho, exhibits characteristics which initially suggest potential for management as a pollinator in forage and hybrid vegetable seed production. This paper records the first portion of our detailed studies on the biology of this subspecies.

The species is found nesting gregariously in well-defined "bee beds." Like most others of more than 90 species of *Melissodes*, *M. t. tepida* biology has been unknown. LaBerge (1956a, b) reclassified the *M. tepida* complex into three subspecies, *M. t. tepida* Cresson, *M. t. timberlakei* (Cockerell) and *M. t. yumensis* LaBerge, and mapped the geographic ranges of each. Recent papers recording details on nesting habits of other *Melissodes* species, and serving as background information for our studies, include Hurd and Linsley (1959), Evans and Linsley

(1960), LaBerge (1961, 1963), Butler et al. (1962), Thorp and Chemsak (1964), Clement (1973), Batra and Schuster (1977), Buchmann and Jones (1980), Parker et al. (1981), Tepedino and Parker (1982), and Bouseman (1987). Refer to Thorp and Chemsak (1964), Clement (1973), and Buchmann and Jones (1980) for list of earlier recorded publications on *Melissodes* spp. biology.

Linsley (1946) has presented the only previously recorded information on the biology of the species.

Ours and other collecting records indicate *M. t. tepida* is a polylectic group with preference for visiting flowers of the families Euphorbiaceae, Lamiaceae, Fabaceae, and the composite genus *Gutierrezia*.

NESTING SITES

Two nesting sites near Parma, Canyon County, Idaho, were selected for field studies and as a source of laboratory material. Site 1 was a 2 m × 30 m strip along the southern edge of a farm road. *Distichilis striata* (Torr.) Rydg., a salt grass, provided

the only vegetative cover overlaying the entire site in varying density. The soil is a Moulton sandy loam saline with the top 5–6 cm a mixture of litter and sandy loam, and with moist sandy loam densely packed beneath. *D. stricta* roots and rhizomes are found matted to a depth of over 20 cm throughout the site. Site 2, nearly 4 km from site 1, was approximately 90 m square with an evenly, densely distributed cover of *D. stricta*. The site was otherwise markedly similar to site 1 in soil characteristics.

METHODS AND MATERIALS

Twelve equal-sized plots delimited by plastic stakes were established at each site. Wind velocity was recorded continuously during field observation periods using anemometers set at elevations of 30 cm, 1 m and 2 m. Humidity and temperature data were also recorded. At site 1, soil temperatures were monitored at depths of 5, 10, 15, 20, 25 and 30 cm beneath the surface using copper-constant thermocouples recording directly through a Leeds and Northrup potentiometer.

Early field observations centered upon determining emergence periods of *M. t. tepida* and associated insects. Metal screen mesh emergence cages (1.5 × 2 × 1 m) distributed randomly on the sites were used to trap the emerging insects. Daily checks were made, data recorded, and trapped specimens were then released.

To facilitate tracking individual bee activity, specimens were captured with nets, dusted with a powdered, daylight, fluorescent dust (trade name Day-Glo) and released. Three distinctive colors were used: neon-red, fire-orange, and arc-yellow. After release, individual bees were easily observed and the color identified at distances up to 10 m. This pigmented powder was also used to follow construction of burrows. Selected burrows were tagged by placing numbered plastic stakes near each entrance. Each numbered burrow was then dusted with Day-Glo. The burrows were marked

from three to six times at intervals during the day using an aspirator bulb and directing the powder into the burrow through a tapered glass nozzle. Movements of earth in the burrow and accompanying brushing action by females distributed the powder throughout the burrow. Their excavating and burrow sealing activities incorporated the dust into the plugging material of the laterals and the cells walls. In addition, females returning from foraging were dusted before entering a marked burrow. Using this burrow-marking technique, 51 nests were dusted and studied over the two-year study period.

Each fall all marked burrows were excavated using a standardized technique which exposed the details of burrow construction. The technique consisted of digging a trench, with a 45 cm deep vertical face 30 cm from the burrow entrance. Using a small knife, brush, and air tubing, each burrow was exposed step-by-step from the entrance to the distal cells. A model of each burrow was then constructed. Exposure of the burrow construction was always complicated by the maze of *D. stricta* roots.

All cells removed from excavated burrows were placed in plastic cups, numbered, stored in a styrofoam cooler, and taken to the laboratory for detailed examination. Over two hundred cells were removed and used in the laboratory studies to supplement observations and experiments conducted at the nesting sites. These studies concentrated primarily upon anatomical evaluations of the life stages, determination of developmental stadia reared under controlled temperatures, and observations on larval feeding. Results of the laboratory studies are being presented in a subsequent paper.

Female activity at the nesting site was charted continuously, including timing the periods of foraging and nest construction. Cylindrical screen cages (30 cm diameter) were placed over individual burrows. As a marked female emerged from the burrow or approached the burrow subsequent to foraging, the cage was removed, allowing ac-

tivity of that individual to continue. Each phase of insect activity was recorded. Stop watches were used to time the activity intervals.

Pollen was removed from a sample of cells and from pollen loads on females at irregular intervals as the bees returned from foraging. Pollen slides were prepared for microscopic examination to determine the pollen sources employing the MacCallum-Goodpasture method which uses a gentian dye for staining and consequently highlighting individual pollen grains.

BIOLOGY

Adult emergence.—Following ecdysis from the pupal case, teneral adults commonly remained in the cells for several days before burrowing to the surface. During emergence the bees chewed through the cocoon and fecal cap, and burrowed vertically through the soil leaving the old cell filled with the shredded cocoon, fecal material, and soil. Emerging bees remained in the mouth of the exit burrow approximately 24 hours before beginning flight activity. *M. t. tepida* exhibited protandry with males emerging and establishing territorial flight patterns over the nesting site approximately seven days prior to emergence of the first female bees. However, some overlap in the range of emergence times for male and female bees did occur.

At the first nesting site, emergence began at the west end of the site and extended to the east end over approximately a two-week period. Increase in plant cover on the site west to east influenced soil temperature and undoubtedly accounted for differences in emergence times. Soil temperature records taken at varying soil depths in the site supported this conclusion.

Male bees began actively establishing flight patterns over the nesting sites in early July. Excavation of nest samples at the time of first male emergence exposed both developing pupae and female adults ready to emerge.

The normal life span of adult male bees generally varied from 12 to 15 days (average 14 days). Two weeks after initial emergence, a decline could be noted in the number of male bees present at the sites, and by the end of July few males were observed. The normal life span of the female ranged from 18 to 23 days with an average of 20 days. With the range in the emergence times, nesting activity continued through early August.

Male flight activity.—The flight activity of male *M. t. tepida* following emergence exhibited a basic territorial behavior pattern. The individual bee defended an area 14 cm to 30 cm in diameter from intrusion by other male bees. A male would chase an intruding bee for a distance of up to 3 m from the defended area, and then return.

Male bees, captured and removed from their territory and released elsewhere on the site, would return to their original area of activity usually within 30 minutes.

Mating.—Male aggressiveness was displayed in its mating behavior. As virgin females emerged from their burrows, they were literally pounced upon by the males either before they took flight or as they began to fly. Virgin females which attained flight were knocked back down to the ground. In many cases a newly emerged female accepted the male's attempt to copulate without rejection. All mating took place on the ground. The male mounted the female dorsally with his prothoracic legs grasping the female around the mesothorax and his mesothoracic and metathoracic legs hooked around the female's abdomen. During copulation the male displayed two different pulsating actions of his abdomen. Commonly, first pulsations were very rapid and short, lasting from five to ten seconds in duration. Following this, pulsations became slower and stronger, lasting approximately ten seconds. During these copulatory activities the antennae of the male came in contact with the female's antennae, but no definite stroking patterns were noted. The total period in copula ranged from 40 to 65

seconds with an average of 45 seconds. Following copulation the female departed and began nesting activity.

Mated females remained attractive to all males for a few days following copulation. This suggests a probable sex attractant secreted by the female. During this period of continued attraction, as females approached their burrows carrying pollen, males would dart from an established flight pattern, knock females to the ground and attempt copulation. These copulatory attempts were repulsed by the females who freed themselves within seconds and resumed nesting activity. Mated females became less attractive to males with time and, after approximately one week following copulation, they were ignored by male bees as they flew about the nesting site.

On two occasions during our extensive nesting site observations, males were seen attempting copulation with other males. In each case contact between the two males was terminated within a few seconds.

Sleeping behavior.—Males slept at the nesting site, finding shelter under debris or at the entrance of a female nesting burrow. In a burrow, males slept with their heads positioned outward. Females always slept in the burrow. Excavation of burrows after 10:30 pm exposed inactive females in the lower distal portion of the burrow.

Daily activity.—Although both soil temperatures and air temperatures were recorded at nesting site 1, it was difficult to determine specific temperature thresholds for *M. t. tepida* activity. Generally, air temperatures reached 21°C before full bee flight activity was observed. At air temperatures above 36°C activity was greatly reduced, although a few individuals remained active at temperatures of 38°C. Bee flight activity was much reduced when wind velocities exceeded 24 km per hour. Normally male bee activity began between 9:00 am and 9:30 am and continued throughout most of the day. It gradually decreased following 1:00 pm and ceased by 5:30 pm. Female bee for-

aging activity began between 10:00 am and 10:30 am. Generally, foraging activity reached a maximum by 11:00 am, decreased sharply between 1:00 pm and 2:00 pm, and continued to decline during the afternoon as females spent more time in the burrows. Foraging activity virtually ceased by 6:30 pm. During the course of these studies two non-foraging females were observed returning to the nesting site after 6:30 pm.

Nest construction.—Female *M. t. tepida* constructed and provisioned individual burrows. Generally, a female constructed only one burrow during the season, but some females were observed excavating a second or even a third burrow in the event of destruction or obstruction of the burrow entrance.

This subspecies showed a tendency to construct entrances at the edge of rocks or other ground debris, although some bees burrowed in open areas covered only by the salt grass vegetation. In areas supporting large numbers of females, entrances were frequently 2.5 cm to 12 cm apart, while in less active areas distances between holes frequently varied from 0.3 m to 2 m. When numerous rocks were placed on the ground in a central area of bee activity, small aggregations of female bees, sometimes as many as seven, began constructing burrows at the edge of the rocks.

While initiation of nest construction at the sites was noted at many differing hours throughout the day, the majority of females began nest construction during the morning hours subsequent to 10:30 am.

Once a female had chosen an area for nest construction, she landed and began scratching vigorously with the prothoracic legs, kicking the soil behind the abdomen with these and the mesothoracic legs. She quickly penetrated the soil surface and removed the dirt from the main shaft as she backed out of the burrow. Tumulus formed by the removal of the soil from the main shaft was dissipated in a few days with weathering and bee activity about the entrance. Below the



Fig. 1. Section of a soil profile from site 1 exposing the main shaft and lateral of a *M. t. tepida* nest. Note cell beneath lateral and partial outline of a second lateral and cell extending from first lateral.

first 5 cm of soil the ground became increasingly more compacted. Here the female was seen to use a twisting action of the head, loosening the soil particles with her mandibles. Following completion of the first cell, the female began excavation of a second lateral, at an angle out from the main shaft. Dirt excavated from this lateral was repacked into the first lateral completely plugging it to the main shaft.

Nest description (Fig. 1; Fig. 2A, B; Fig. 3A–C).—The open circular entrance (diameter 7 mm) had no turret. The burrow was formed at angles approaching 90° to soil surface with the main shaft (diameter 6 mm) extending to a depth of 7 to 13 cm. Laterals branched out from the main shaft at different levels at angles of 15° to 90° from the main burrow. The distal end of each lateral was curved and widened to 7 mm and ended in a single, vertical cell. Depths of cells ranged between 10 and 20 cm beneath the

soil surface at both nesting sites. The main shaft and the laterals were smooth-walled but lacked a lining as found in the cell. In constructing a cell, the female first “roughed out” the cell to a diameter of 1.4 cm, then repacked the soil leaving a hard, smooth crust lining the cell wall. The finished cylindrical cell (diameter 7 mm, length 15 mm) had a rounded base and tapered near the top to about 6 mm in diameter. The specially constructed cell was found to be highly resistant to water penetration.

Provisioning.—The female transported unmoistened pollen on the scopal hairs of the metathoracic legs. She approached her nest, landed near the opening, and entered the burrow immediately. In the burrow a female must reverse position either at the widened distal end of the lateral or within the nest cell in order to deposit the pollen load at the base of the cell. The female removed the pollen load by rubbing the meta-

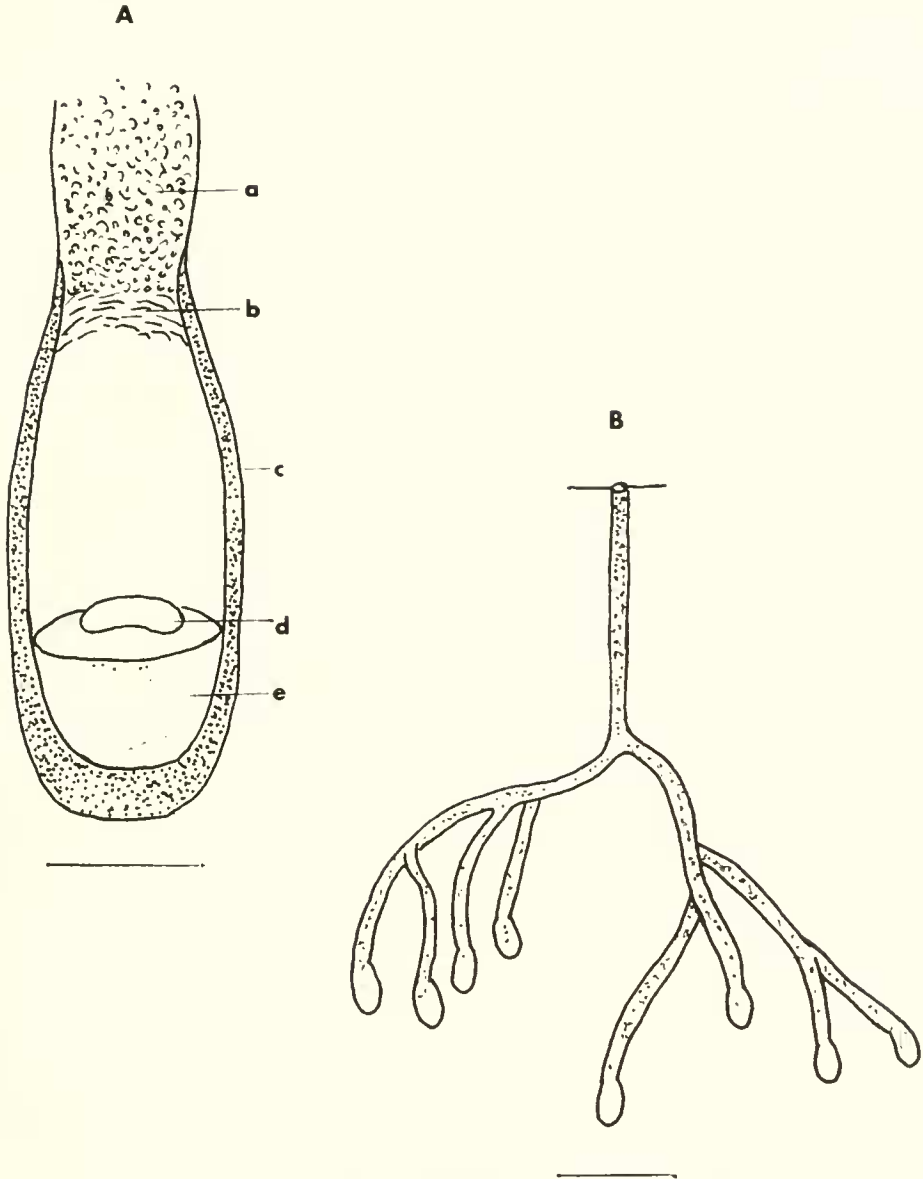


Fig. 2. A. Drawing of enlarged nest cell of *M. t. tepida* to illustrate (a) plugged lateral, (b) spiraled cell cap, (c) repacked and mixed cell wall, (d) egg, (e) pollen mass. Bar equals 0.5 cm. B. Illustration of generalized nest of *M. t. tepida*. Bar equals 4 cm.

thoracic legs against the abdomen and utilizing the lever action of the tibial spurs of the opposing leg. Later, after the female had completed stocking that cell, she mixed the pollen mass with nectar and packed this larval food into a semi-solid mixture, leaving the upper surface slightly concave. These

pollen masses occupied about 30% of cell volume in the lower portions of cells examined and averaged 4.5 grams in weight. During embryogenesis the pollen-nectar mixture fermented, forming a semi-liquid mass which increased in volume.

Pollen samples extracted from cells or re-

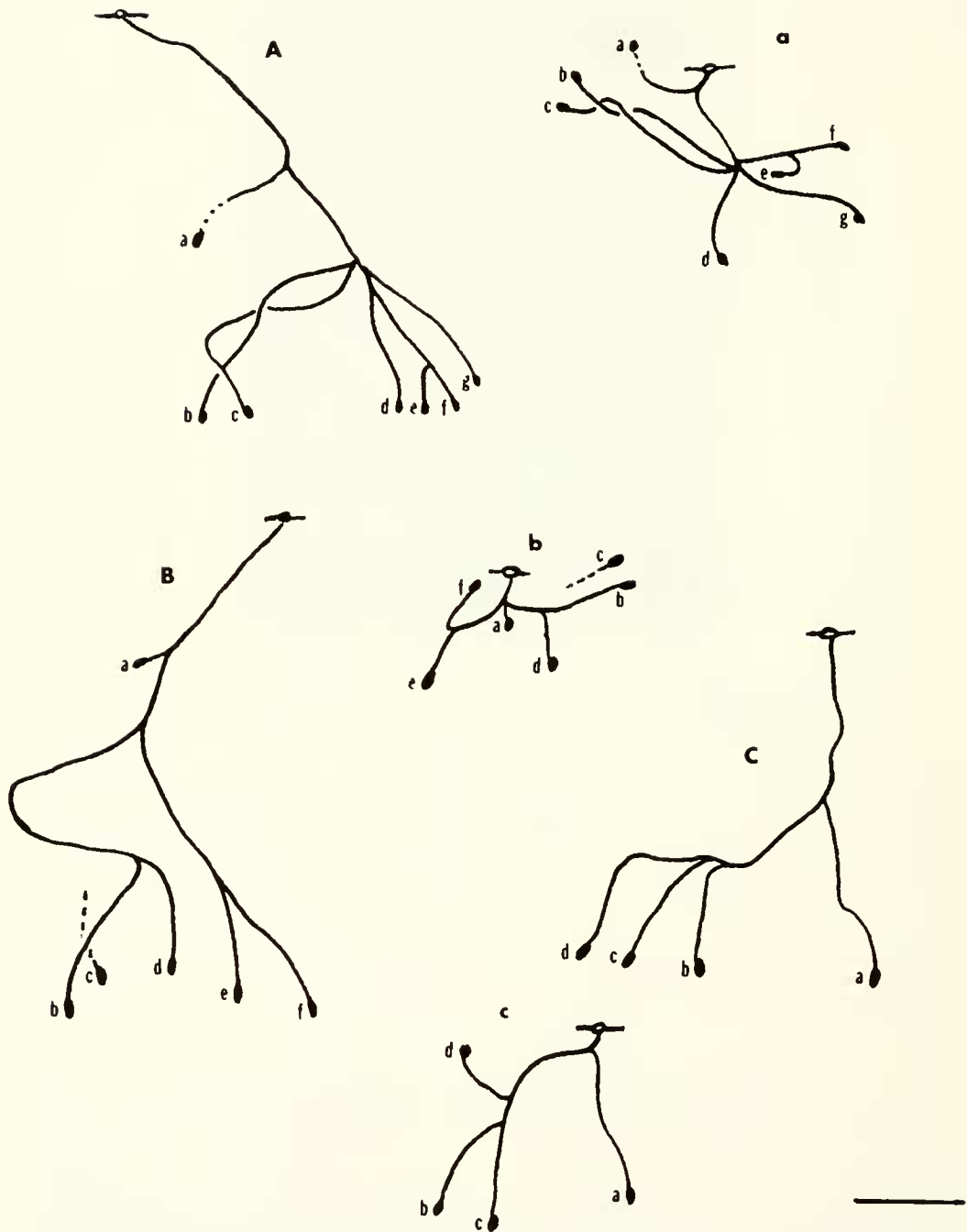


Fig. 3. Schematic sketches of three nests of *M. t. tepida* reconstructed after excavations during this study. A.B.C. Lateral aspects of three nests. a.b.c. Dorsal aspects of same nests. Bar equals 4 cm; —○— represents burrow entrances.

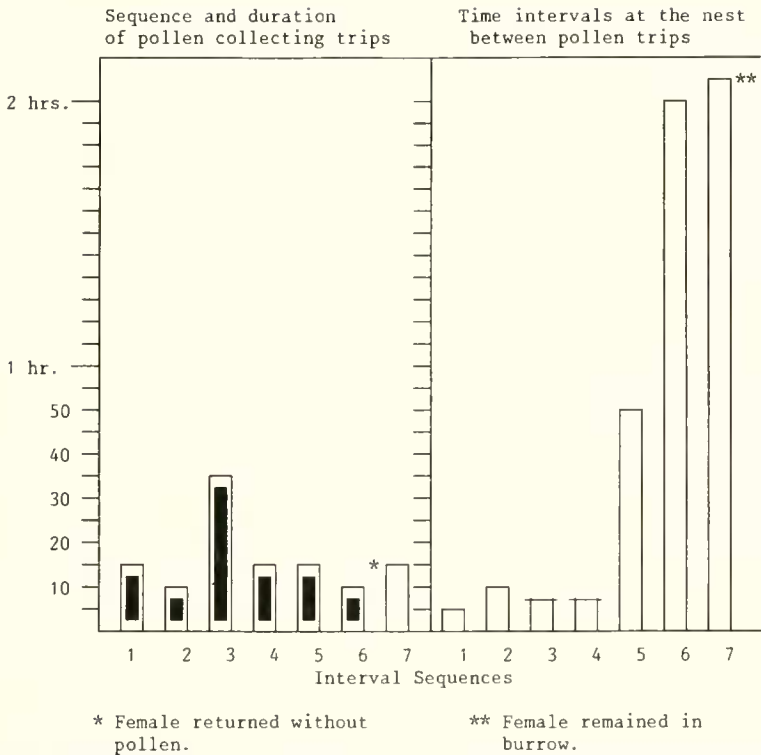


Fig. 4. Histogram illustrating a typical time sequence of foraging and at nest activities by an individual female *M. t. tepida* in stocking a single cell.

moved from foraging females were collected from several species of Fabaceae (*Medicago sativa* L., *Melilotus officinalis* (L.) Pall., *Trifolium* sp.), an Asteraceae species *Gutierrezia sarothrea* (Pursh) Britt. & Rusby., and a Chenopodiaceae *Atriplex* sp., verifying that female *M. t. tepida* are indeed polylectic.

Our records established that 5–6 foraging trips by a female were required to provision a nest cell. The time spent collecting pollen in the field varied from 13 minutes to 35 minutes per trip with an average time of 15 minutes. The average period of time required for depositing a pollen load was approximately six minutes. As the female neared completion of cell provisioning, she often remained in the burrow for longer periods of time, mixing and packing the pollen-nectar mass or resting. A graphical presentation typical of the time sequence of foraging and pollen deposition for a single

cell by an individual female bee is illustrated in Fig. 4. The authors did not observe any variation in female foraging times as correlated to plant species visited.

SUMMARY AND DISCUSSION

The extent of variability in the behavior patterns among *Melissodes* species is noteworthy. Nesting of *M. t. tepida* appears restricted to alkali soils. This differs from reports for other species in the genus, but agrees with other species in that all nest in soils with a sandy surface and moist compacted soil below. Others have found species generally nesting in bare soil areas while *M. t. tepida* was found on sites reasonably well-covered by *Distichilis stricta*, an alkaline soil indicator plant. Nesting is aggregated displaying a tendency for concentration of burrows under ground debris or along edges of rocks or soil clods. Females were not seen

to share burrows or burrow entrances and did not plug those entrances until the completion of the foraging period. Unlike some species reported to construct single cell burrows, *M. t. tepida* develops multicelled nests and coats each cell with a waterproof lining which, we suspect, from Batra and Hefetz studies (1979), is of acetate material from Dufour's gland. They stock these cells about one-third full with pollen mixed with some nectar and compacted into a cylinder with a concave surface.

Males begin to emerge from southwestern Idaho nesting sites in early July and establish flight patterns of a territorial-like nature a week prior to female emergence. Females begin emerging in mid-July and nesting activity extends to about mid-August.

Our studies of the pollen sources showed *M. t. tepida* to be polylectic, visiting a variety of host plants for pollen including *Atriplex* sp., *Gutierrezia sarothraea*, *Medicago sativa*, *Melilotus officinalis*, and *Trifolium* spp. Studies of pollen samples revealed a preference for *Atriplex* sp. Because of the relatively small populations in this area and the fact that the legumes comprise only 5% to 10% of the pollen collected for cell provisioning, the economic value of *M. t. tepida* as an important pollinator remains questionable. Nevertheless the fact these insects form nesting aggregations in a specific nesting medium and are relatively polylectic offers potential for manipulation in hybrid seed production, especially under large cage management conditions. Further study and experimentation with this potential is desirable.

ACKNOWLEDGMENTS

The authors express their appreciation to G. E. Bohart, Logan, Utah for his species determinations, and to him, M. A. Brusven and G. W. Bishop, University of Idaho, for their advice on the study. We are also indebted to A. L. Steinhauer and F. G. Wood, University of Maryland, and to J. B. Johnson and M. Rice, University of Idaho, for their valuable assistance with this manu-

script. Contribution No. 88721 from the University of Idaho, Agricultural Experiment Station.

LITERATURE CITED

- Batra, S. W. T. and A. Hefetz. 1979. Chemistry of the Cephalic and Dufour's gland secretions of *Melissodes* bees. *Ann. Entomol. Soc. Am.* 72(4): 514-515.
- Batra, S. W. T. and J. C. Schuster. 1977. Nests of *Centris*, *Melissodes* and *Colletes* in Guatemala (Hymenoptera: Apoidea). *Biotropica* 9(2): 135-138.
- Bouseman, J. K. 1987. Collection of *Melissodes* (*Apo-melissodes*) *apicata* in Illinois (Hymenoptera: Apoidea). *J. Kans. Entomol. Soc.* 60(2): 335-336.
- Buchmann, S. L. and C. E. Jones. 1980. Observations on the nesting biology of *Melissodes persimilis* (Hymenoptera: Anthophoridae). *Pan-Pac. Entomol.* 56(3): 200-206.
- Butler, G. D., Jr., F. E. Todd, S. E. McGregor, and F. G. Werner. 1962. *Melissodes* bees in Arizona cotton fields. *Arizona Univ. Agr. Exp. Sta. Tech. Bull.* 139: 1-11.
- Clement, Stephen L. 1973. The nesting biology of *Melissodes* (*Eumelissodes*) *rustica* Say, with a description of the larva (Hymenoptera: Anthophoridae). *J. Kans. Entomol. Soc.* 46(4): 516-525.
- Evans, H. E. and E. G. Linsley. 1960. Notes on a sleeping aggregation of solitary bees and wasps. *Bull. So. Calif. Acad. Sci.* 59: 30-37.
- Hurd, P. D. and E. G. Linsley. 1959. Observations on the nest site behavior of *Melissodes composita* Tucker and its parasites, with notes on the communal uses of nest entrances (Hymenoptera: Apoidea). *Entomol. News* 70: 141-146.
- LaBerge, W. E. 1956a. A revision of the bees of the genus *Melissodes* in the North and Central America Part I. *Univ. Kans. Sci. Bull.* 37(2): 911-1194.
- . 1956b. *Ibid.* Part II. 38(1): 533-578. 1957.
- . 1961. *Ibid.* Part III. 42(5): 283-663.
- . 1963. New species and records of little-known species of *Melissodes* from North America. *Univ. Nebr. State Mus. Bull.* 4: 227-242.
- Linsley, E. G. 1946. Insect pollinators of alfalfa in California. *J. Econ. Entomol.* 39: 18-29.
- Parker, F. D., V. J. Tepedino, and G. E. Bohart. 1981. Notes of the biology of a common sunflower bee *Melissodes agilis*. *J. New York Entomol. Soc.* 89(1): 43-52.
- Tepedino, V. J. and F. D. Parker. 1982. Interspecific differences in the relative importance of pollen and nectar to bee species foraging on sunflowers. *Environ. Entomol.* 11(1): 246-250.
- Thorp, R. W. and J. A. Chemsak. 1964. Biological observations on *Melissodes* (*Eumelissodes*) *pallidisignata*. *Pan-Pac. Entomol.* 40: 75-83.